



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at ScienceDirect

Hormones and Behavior

journal homepage: www.elsevier.com/locate/yhbeh

Social status and cortisol levels in singing rock hyraxes

Lee Koren^{*}, Ofer Mokady, Eli Geffen

Department of Zoology, Tel Aviv University, Tel Aviv 69978, Israel

ARTICLE INFO

Article history:

Received 14 January 2008

Revised 21 February 2008

Accepted 23 February 2008

Available online 8 March 2008

Keywords:

Mating success

Procavia capensis

Stress hormones

Stress of domination hypothesis

Vocalization

Social rank

ABSTRACT

Many mammals use acoustic signals to communicate with conspecifics. Rock hyraxes (*Procavia capensis*) are social mammals whose vocal communication is usually restricted to quiet sounds used between nearby individuals. Loud repetitive warning trills are an exception. In our study site, a third of the adult male hyraxes also produces a rich, complex and loud vocalization we term 'singing'. In this study, we examine whether singers, which are more conspicuous by the act of singing, have higher cortisol (i.e. basal stress; C) levels than non-singers, and whether there is an association between social status and stress hormones in male hyraxes. We show that 'singing' males are different from the general adult male population in that their C levels are higher than those of silent males. Only in singers, C levels are associated with social rank, with dominants showing the highest levels. Singers are also on average older and more dominant than most other sexually mature non-singing males. Further, they copulate more than non-singers, suggesting that singing males may have higher reproductive success. Our results support the 'stress of domination' hypothesis and indicate that in the rock hyrax singing may reflect high competitive ability, designating singers as a distinct class of males, unique in their personal attributes and behavior.

© 2008 Elsevier Inc. All rights reserved.

Introduction

Several studies have demonstrated a tight link between social rank and concentrations of stress-related hormones. For example, basal glucocorticoid levels in free ranging social mammals are usually higher in dominants than in subordinates (Barrett et al., 2002; Carlson et al., 2004; Cavigelli et al., 2003; Creel et al., 1997, 1996; Creel, 2005; Gruenewald et al., 2006; Mooring et al., 2006; Muller and Wrangham 2004b), although there are exceptions (Sapolsky, 1993). This phenomenon of high stress hormones in high-ranking individuals is termed the 'stress of domination' hypothesis. During the mating season, dominant and more aggressive males in many mammals and birds show higher territorial and sexual behaviors, such as singing, aggression and courtship display (Creel et al., 1997; Ketterson and Nolan, 1992; Muller and Wrangham, 2004a; Sapolsky, 1982). The act of singing by itself may therefore be a means to communicate information on social status and hormonal state (Galeotti et al., 1997).

The significance of vocal communication, especially male vocalization, has been addressed in numerous animal systems (Andersson, 1994). Many mammals use acoustic communication that is termed 'calling' (Clutton-Brock and Albon, 1979; Fischer et al., 2004; McElligott and Hayden, 1999). Unlike birds, mammals rarely sing as such (i.e. long, complex vocalizations, typically composed of consistently repeated syllables; Spector, 1994). Song has only been attributed to a few primates (Tenaza, 1976), marine mammals (Payne and McVay, 1971), bats (Davidson and Wilkinson, 2004) and rodents (Holy and Guo, 2005),

and may be used to communicate with their group members or with strangers (e.g., McComb et al., 2003; Walcott et al., 2006).

In social mammals, males expend vast amounts of energy in order to appear attractive and to advertise themselves as successful mates. Animals that use elaborate displays and thus potentially endanger themselves, advertise their quality to both male and female conspecifics (Zahavi, 1977). Singing, which may be a form of advertisement (Zahavi, 1977), can be expensive in terms of time and energy investment and in terms of increased predation risk (Ryan et al., 1982; Tuttle and Ryan, 1982). Consequently, the act of singing may also be under intense selection, and performed only by these individuals that can bear its consequences (Zahavi, 1977; Kotiaho et al., 1998; Wagner, 2005).

Rock hyraxes are social, live in large, mixed-sex groups, and often communicate acoustically (Fourie, 1977). Both male and female hyraxes produce loud repetitive warning trills, whereas it is mostly adult males, but not all males, that engage in diverse vocalization (Fourie, 1977; Hoeck et al., 1982; Koren, 2000) we term 'singing' (see Supplementary material). Like birds, bats and gibbons (Behr et al., 2006; Hyman, 2003; Tenaza, 1976), hyraxes often engage in counter-singing with neighboring males (Koren, 2000). Rock hyraxes in our study site, Ein Gedi, are subjected to predation by leopards, hyenas and wolves (Koren, 2000).

In this study, we examined three hypotheses: 1. Singers (i.e., vocalizing males) have higher cortisol (i.e. basal stress) levels than non-singers. The act of singing may attract more potential predators to the singer (e.g. Rasa, 1986; Ryan et al., 1982), which in turn elevates its stress level. 2. Singers are more dominant than non-singers. This hypothesis predicts that singers have higher competitive abilities than non-singers.

^{*} Corresponding author. Fax: +972 3 640 7304.
E-mail address: leezi@post.tau.ac.il (L. Koren).

3. 'Stress of domination' hypothesis — there is a relationship between social status and stress hormones in male singers. We predict that high-ranking singers have higher stress hormone levels than low-ranking singers.

Methods

Study animals

Rock hyraxes (*Procavia capensis*) have been studied by us in the Ein Gedi Nature Reserve, west of the Dead Sea in the Judean Desert, Israel (31°28'N, 35°24'E), since 1999 as part of a long-term study. Permits for capturing and handling the hyrax were issued and reviewed annually by the Israeli Nature and Park Authority. The data presented in this paper pertaining to male hyrax songs were collected for 6 months annually (February–August; i.e., a month before parturition until the end of the mating period) over five consecutive years (2000–2004), under permit numbers: 2000/8871, 2001/8871, 2002/14674, 2003/14674, 2004/17687.

Hyraxes are mostly diurnal, and at this study site they are relatively habituated to the presence of humans. They are seasonal breeders with synchronized births (Mendelssohn, 1965). Mate guarding and manipulation by the territorial male thus appear to be limited, probably offering subordinates an opportunity to occasionally sire offspring as well (Emlen and Oring, 1977). Sexual maturity, is reached at about 16 months of age (Mendelssohn, 1965), after which most adolescent males (17–24 months old) are forced to disperse (Hoeck et al., 1982), joining bachelor groups (Koren et al., 2006). Mixed-sex groups in Ein Gedi comprise several males (one mature immigrant and several natal late dispersers), and between ten and twenty females with their pups. The immigrant 'resident' male may stay with a group for a few years before being evicted and replaced by another male.

Morphometrics

All males were caught using live box traps, which were placed in natural crevices. Traps were set open before first light (approximately 90 min before dawn) and operated until noon, with inspections every 2 h. New males were anesthetized with ketamine hydrochloride, which sedated the animals to a state that allowed safe handling. Each male was individually marked using a collar (collar weight 5 g; range of 0.125% to 0.2% of hyrax body weight). Body length (base of the skull to tip of the tail), head diameter (at eye level), body girth and weight were taken for each animal as size indicators. After marking and measuring, hyraxes were returned to the traps for full recovery (3 h), following which they were released at the capture site. Animals resumed full normal activity following their release. We combined hyrax body length, head diameter and body girth into a single morphometric variable using principle component analysis (PCA). That first component in the PCA explained 90.5% of the variance in our morphometric data (Eigenvalue=2.7).

Age

All births at Ein Gedi are in the spring, with pups first observed in March. The birth year for all natal males was known since they were captured as pups. Body weight (BW) was the best predictor of known age in 89 males using linear fit (age was normalized using the Box–Cox transformation; normalized age = $0.971 + 1.681\text{BW}$; $r^2 = 0.925$, $F_{(1,88)} = 1092.6$, $P < 0.0001$; Koren, 2006). Using the above equations, we estimated the age of immigrants and individuals born before our study began in 1999.

Social hierarchy and singing behavior

Behavioral observations were recorded over a five-year period, for a total of 430 observation days and approximately 3000 h (by LK), using 10×42 binoculars and a telescope with ×50 and ×75 magnifications. Most observations were in the morning from dawn until noon (approximately 6 h); thereafter hyraxes retreat from the heat, resuming activity once the canyon is shaded (afternoon session; approximately 2.5 h long). All agonistic interactions among individuals belonging to 6 social groups were recorded (all occurrences; Altmann, 1974), and the initiator, recipient and outcome were specified. Only agonistic interactions that involved display by one individual (i.e. approaching, biting, pushing or chasing) and resulted in an evasive action being taken by a second animal (i.e. running away or retreating from position) were considered for the social hierarchy analysis. A matrix of encounters was prepared for each group using all pairwise agonistic interactions observed during a given field season. Social hierarchy was calculated from the interaction data using David's score, which take into account the wins and losses of the focal individual and its opponents (Gammell et al., 2003; Excel macros by H. de Vries). In addition, each animal was ranked using the calculated David's scores. The animal with the highest score was ranked first (i.e. 1), the next was ranked second (i.e. 2), etc. All scores and ranks were normally distributed.

Singing behavior in our study area gradually starts in February (pre-parturition), peaks in August (mating period), and ceases abruptly after. Singing males were observed in the morning sessions, when sound propagation is at its peak (Titze, 2000). In Ein Gedi, daily strong afternoon winds interfere with sound recordings. Singing is loud and can be heard up to 500 m away from the singer (LK, unpublished data). Songs last a few minutes, allowing for the observer to locate and identify singer. The time,

singer and social situation during which it was recorded were noted. We defined males as singers only if the singer was directly observed and identified.

Hormone levels

We measured the basal levels of the stress hormone cortisol (C) that accumulated over a period of a few months in the hair of male rock hyraxes. Hormones are deposited in a growing hair shaft by the blood vessel that feeds it. Hair-testing has the advantage of being insensitive to the momentary stress of capture (Yang et al., 1998), while accurately assessing significant and prolonged stressful experiences (Davenport et al., 2006). Hair samples were cut once a year (April–July; pre-mating period), from the back leg of trapped hyraxes in the field, without the need for sedation. The extraction protocol followed the steps in Koren et al. (2002). All samples collected for each year were analyzed as a single batch. Hair from each individual was tested in duplicates in a double-blind experimental set-up. The steroid hormone was detected using a competitive ELISA method (human cortisol saliva kit; DRG International; NJ, USA). The kit was validated for use with this species by demonstrating parallelism between serial dilutions of hyrax hair and the standard curves generated with kit calibrators. Cross reactivity of the cortisol antiserum was 100% for cortisol and 60% with prednisolone, 29% with corticosterone, 3% with cortisone and less than 1% with any other naturally occurring steroid hormones. The mean coefficient of variation between C assays ($n=6$) was 8.3% and within the same assay ($n=6$) was 4.6%. Unlike serum or saliva, hormones from hair need to be extracted by solvents, sonicator, and other manual steps. Since slight variations in the extraction protocol between sets of samples may influence the final concentration detected, we compared hormone levels across areas and years by standardization (z-score) of each ELISA-plate.

Statistical analysis

All comparisons between singers and silent males were carried out using the parametric t-test (two tailed; unequal variance). C levels were normalized by $\log(x^2)$ transformation. Since age was the only variable not normally distributed, we calculated probabilities for it using permutation tests (StatXact v. 6; Cytel Statistical Software & Services).

Results

In our study area, only about a quarter of the bachelor males (9 of 35), and all of the resident males ($n=10$) living in mixed-sex groups sang. Resident males that had stopped singing disappeared shortly thereafter (LK, per. obs.). Singers were involved in more than 3 times the agonistic interactions than silent males (79 and 24 aggressive interactions, respectively). Further, singers were involved in all but one of the 25 copulations we observed (total of 13 males). Relative to

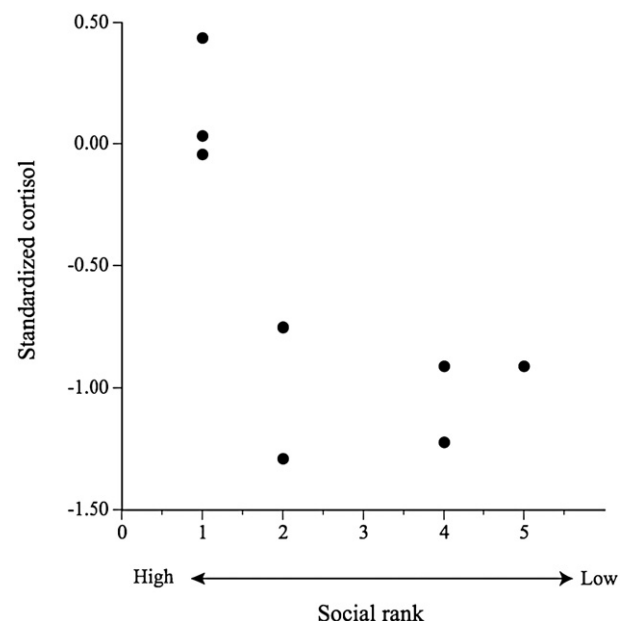


Fig. 1. Standardized cortisol as a function of social rank (using David's score) in male singers. Cortisol levels were non-linearly related to rank ($y = 1.579/x - 1.510$; $r^2 = 0.788$, $F_{(1,6)} = 22.4$, $P = 0.003$).

their availability in the population, singers have significantly higher copulation rate than silent individuals (Fisher exact test; $P=0.0043$). Most singers were immigrants while most silent males were natal males (Fisher exact test; $P=0.0764$).

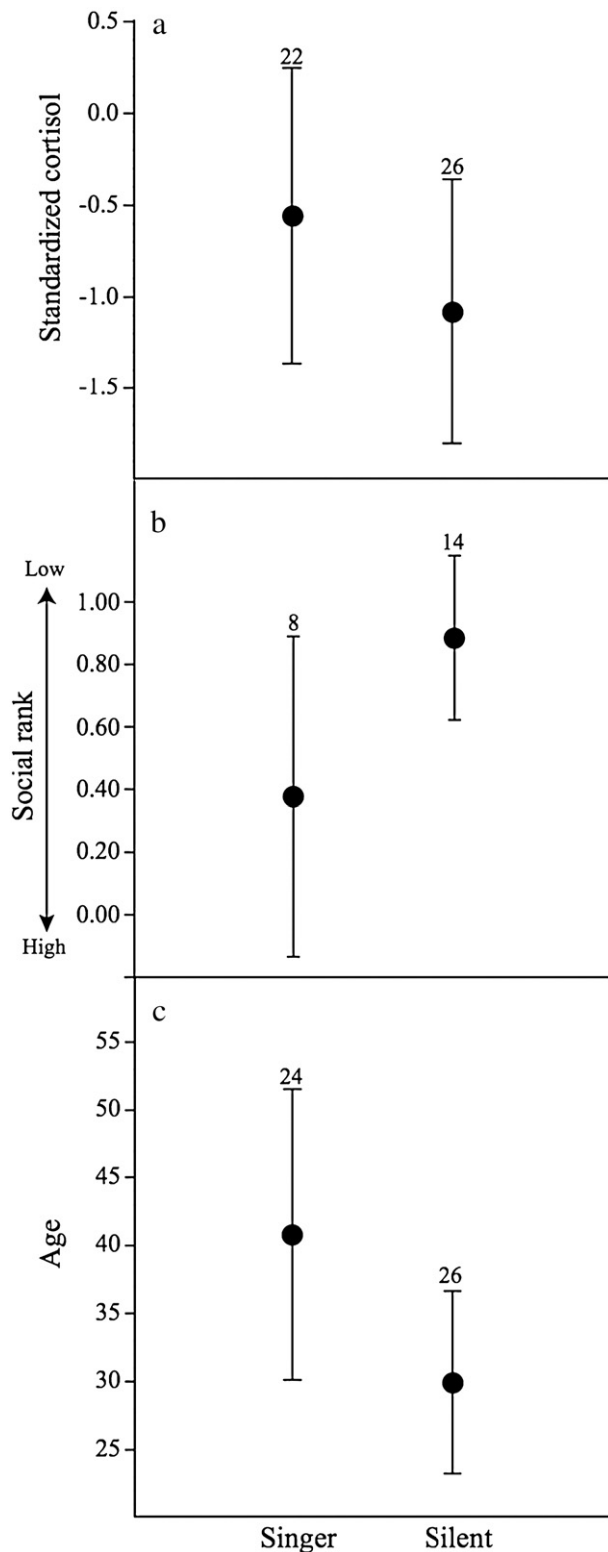


Fig. 2. Adult singers and silent males compared in their average (\pm SD) standardized cortisol levels (a; $t_{(43)}=2.35$; $P=0.02$), rank position (b; $t_{(9)}=2.8$; $P=0.02$) and age (c; $t_{(38)}=4.26$; $P=0.0001$). Sample size is shown above SD bars. Ranks were determined using David's score, whereas dominant hyraxes (ranked 1st or 2nd) were classified as 0, while submissive (3rd or lower) were classified as 1. Age is indicated in months.

We related social status of males with their C levels. Singers, whether belonging to a bachelors or a mixed-sex group, form a unique subpopulation within males. Compared with non-singers ($r^2=0.002$, $F_{(1,8)}=0.016$, $P=0.902$), singers' C levels were related to their rank positions ($r^2=0.788$, $F_{(1,6)}=22.4$, $P=0.003$; Fig. 1), so that the highest ranking males had the highest C levels (i.e., basal stress levels). Compared to non-singers, singers also had higher average C levels ($t_{(43)}=2.35$; $P=0.02$; Fig. 2a) and were more dominant (i.e. ranked higher in the hierarchy using David's score) than silent males ($t_{(9)}=2.8$; $P=0.02$; Fig. 2b). Individuals that sang were significantly older than males that were silent ($t_{(38)}=4.26$; $P=0.0001$; Fig. 2c). Singers were also, on average, physically bigger than non-singers (i.e. morphometrics component; $t_{(30)}=3.9$; $P=0.0004$), but size differences were due to age (i.e. morphometrics component controlled for age; $t_{(26)}=0.055$; $P=0.96$). Among adult males, age was not correlated with C levels ($r_{(61)}=0.11$, $P=0.409$) nor with social status ($r_{(28)}=-0.04$, $P=0.838$).

Discussion

We found that among males, only in the singer subgroup, C levels were related with social rank; a trend demonstrated in several cooperatively breeding mammals, whereas basal levels are often higher in dominants than in subordinates (reviewed by Creel, 2001). This result supports our third hypothesis, the 'stress of domination' in singers. Because of the possible trade-off with the immune system and the known physiological correlates of prolonged high basal glucocorticoids levels, social stress may be a cost that offsets the benefits of high rank (Creel et al., 1996). There are several possible reasons for the elevated cortisol levels observed in singing hyraxes:

- Social rank** – Singers are more dominant than non-singers, and dominant individuals tend to fight more often than subordinates (Creel et al., 1996). The resulting high C levels are necessary for the short-termed fight-or-flight survival mechanism to operate (Creel et al., 1996). In hyraxes, dominance is indeed achieved via aggressive encounters with other males, which may elevate stress response (and C) levels. This result supports our second hypothesis. High-ranking individuals need to aggressively reassert their dominance over new incoming males. Singing in itself may also constitute a dominance-related behavior, since singers often countering with others, a behavior known to signal aggression (Galeotti et al., 1997; Hyman, 2003). Singing was also often temporally adjacent to fights and chases. The risk of a fight progressing from a singing bout may be a realistic threat since singers were involved in more than 3 times the amount of fights than non-singers. Singers were also injured more than non-singers (only 4 badly injured hyraxes were observed over the years, all of which were singers; LK, unpublished data).
- Predation risk** – Singers, by the actual act of singing, may also expose themselves to both a higher predation risk (Ryan et al., 1982) and to rival males (Hyman, 2003), both of which may raise their C levels. The actual act of singing may constitute risk-taking for wild hyraxes in Ein Gedi because many predators were observed in that site (Koren, 2000). However, large adults, because of their size, are only killed by leopards or wolves, and not by raptors (who were observed preying on pups only; Koren, 2000). Singing in hyraxes is mostly performed from conspicuous posts (e.g., top of a large boulder), a position, which in dwarf mongooses (*Helogale undulate*) subjects sentinels to high predation risk (Rasa, 1986); while in meerkats (*Suricata suricatta*) deems sentinels safe (Clutton-Brock et al., 1999). In our study site, we have observed 71 predation attempts on hyraxes, mostly by wolves and leopards, yet only twice were adult males predated on (of 9 predations, one of

which is known to be a singer). The raised singing position that provides hyraxes with good visibility on any approaching predator, along with their large body size, likely classifies the risk of predation while singing as 'low', making the link between stress response and predation the least probable. Nonetheless, our results indicate that singers have higher C levels than non-singers, probably due to other factors, which taken as a whole support our first hypothesis.

- iii. *Mating success* — Reproduction effort has been documented to relate to variations in stress and glucocorticoid levels (Cavigelli 1999; Mooring et al., 2006; Ostner et al., 2008; Vleugels et al., 1986). In Ein Gedi the hyrax mating season is short (July–August), during which male–male competition is fierce and singing behavior is at its peak. Since nearly all observed copulations were by singers, singers likely had more reproductive opportunities than non-singers. Mating opportunities may elevate C levels directly, as well as challenge neighboring males to aggressively displace a copulating male, thus influencing it as well. This possibility also supports our second hypothesis and prediction.
- iv. *Social support* — Social support has been related to stress levels (Goymann and Wingfield, 2004). In hyrax, singers were mostly immigrant males, some of which integrated into mixed-sex groups, while others joined the bachelor groups. Resident males in mixed-sex groups were often dominated by older females (Koren et al., 2006), and bachelor male hyraxes do not form allies. Therefore, immigrant males probably lack relatives and social support in the study area, a situation known to increase stress levels (Abbott et al., 2003).

In this study we show that in the rock hyrax society, males constitute two behaviorally distinct groups: singers and non-singers. These two groups are markedly different in respect to stress and rank. Cortisol is scaled by rank only in the group of singers; it is independent of rank in silent males. The above results suggest that the association between rank and stress may not only be an overall population or group trend, but may also be restricted to a subpopulation unified by a common denominator (e.g., singer). In spotted hyenas (*Crocuta crocuta*), males are divided into two distinct subpopulations that differ in their dominance and sexual behaviors as well as their circulating hormone levels. In that system, the subpopulations stem from group origin (i.e. natal vs. immigrant males) and show different behavior-hormonal interactions (Holekamp and Smale, 1998). In hyraxes, despite the fact that all resident males are immigrants, a minority of bachelors, some of which are males natal to the study area, sing as well. Being a low-ranking singer (e.g., bachelor) may reflect an alternative strategy to the high-ranking male singers, combining some mating success with low social stress. Since our study is correlative, we also cannot rule out the effects of individual, group, or behavior on stress levels and on endocrine relationships, nor can we assess the hormonal influences on singing behavior itself.

The large variances in singer and non-singer attributes show that age, size and social ranks are not prerequisites to singing. Despite that, we found that singers are, on average, older, larger, and more dominant than male hyraxes that do not sing. Singers have higher C levels, which represent, using our long-term measuring tools (i.e. hair-testing) a chronic high baseline, a state which can provoke detrimental pathologies (Sapolsky, 2005). High social stress in dominant singing hyraxes can be due to rank instabilities during the breeding period, where a flow of new males immigrate to areas that contain mixed-sex social groups. The coupling of the potential advertising behavior (i.e. singing) with the observed elevated reproductive opportunities and the known costs of the related chronic high glucocorticoids levels may be all of the elements that an honest quality-signaling system requires to stably exist.

Acknowledgments

We are obliged to B. Sanzenbacher, I. Aravot, and E. Tauber for their extensive help with the trapping of the hyraxes, as well as to the many project students, field guides and park rangers who helped in the field. We wish to thank the Nature and Parks Authority for their permission to work at the Ein Gedi Nature Reserve and to Ein Gedi Field School for their hospitality and logistic help. We wish to thank G. Koren and T. Karaskov for their help with the hormone analysis. Finally, we are grateful to H. deVries for his assistance with the rank determination, to N. Paz and to two anonymous reviewers for constructively commenting on the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.yhbeh.2008.02.020.

References

- Abbott, D.H., Keverne, E.B., Bercovitch, F.B., Shively, C.A., Medoza, S.P., Saltzman, W., Snowdon, C.T., Ziegler, T.E., Banjevic, M., Garland, T., Sapolsky, R.M., 2003. Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Horm. Behav.* 43, 67–82.
- Altmann, J., 1974. Observational study of behavior — sampling methods. *Behaviour* 49, 227–267.
- Andersson, M., 1994. *Sexual Selection*. Princeton University Press, Princeton.
- Barrett, G.M., Shimizu, K., Bardi, M., Asaba, S., Mori, A., 2002. Endocrine correlates of rank, reproduction, and female-directed aggression in male Japanese macaques (*Macaca fuscata*). *Horm. Behav.* 42, 85–96.
- Behr, O., von Helversen, O., Heckel, G., Nagy, M., Voigt, C.C., Mayer, F., 2006. Territorial songs indicate male quality in the sac-winged bat *Saccopteryx bilineata* (Chiroptera, Emballonuridae). *Behav. Ecol.* 17, 810–817.
- Carlson, A.A., Young, A.J., Russell, A.F., Bennett, N.C., McNeilly, A.S., Clutton-Brock, T., 2004. Hormonal correlates of dominance in meerkats (*Suricata suricatta*). *Horm. Behav.* 46, 141–150.
- Cavigelli, S.A., 1999. Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, *Lemur catta*. *Anim. Behav.* 57, 935–944.
- Cavigelli, S.A., Dubovick, T., Levash, W., Jolly, A., Pitts, A., 2003. Female dominance status and fecal corticoids in a cooperative breeder with low reproductive skew: ring-tailed lemurs (*Lemur catta*). *Horm. Behav.* 43, 166–179.
- Clutton-Brock, T.H., Albon, S.D., 1979. Roaring of red deer and the evolution of honest advertisement. *Behaviour* 69, 145–169.
- Clutton-Brock, T.H., Gaynor, D., McIlrath, G.M., Maccoll, A.D.C., Kansky, R., Chadwick, P., Manser, M., Skinner, J.D., Brotherton, P.N.M., 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *J. Anim. Ecol.* 68, 672–683.
- Creel, S., 2001. Social dominance and stress hormones. *Trends Ecol. Evol.* 16, 491–497.
- Creel, S.F., 2005. Dominance, aggression, and glucocorticoid levels in social carnivores. *J. Mammal.* 86, 255–264.
- Creel, S., Creel, N.M., Mills, M.G.L., Monfort, S.L., 1997. Rank and reproduction in cooperatively breeding African wild dogs: behavioral and endocrine correlates. *Behav. Ecol.* 8, 298–306.
- Creel, S., Creel, N.M., Monfort, S.L., 1996. Social stress and dominance. *Nature* 379, 212.
- Davenport, M.D., Tiefenbacher, S., Lutz, C.K., Novak, M.A., Meyer, J.S., 2006. Analysis of endogenous cortisol concentrations in the hair of rhesus macaques. *Gen. Comp. Endocrinol.* 147, 255–261.
- Davidson, S.M., Wilkinson, G.S., 2004. Function of male song in the greater white-lined bat, *Saccopteryx bilineata*. *Anim. Behav.* 67, 883–891.
- Emlen, S.T., Oring, L.W., 1977. Ecology, sexual selection, and evolution of mating systems. *Science* 197, 215–223.
- Fischer, J., Kitchen, D.M., Seyfarth, R.M., Cheney, D.L., 2004. Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behav. Ecol. Sociobiol.* 56, 140–148.
- Fourie, P.B., 1977. Acoustic communication in rock hyrax, *Procavia capensis*. *J. Compar. Ethol.* 44, 194–219.
- Galeotti, P., Saino, N., Sacchi, R., Moller, A.P., 1997. Song correlates with social context, testosterone and body condition in male barn swallows. *Anim. Behav.* 53, 687–700.
- Gammell, M.P., De Vries, H., Jennings, D.J., Carlin, C.M., Hayden, T.J., 2003. David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. *Anim. Behav.* 66, 601–605.
- Goymann, W., Wingfield, J.C., 2004. Allostatic load, social status and stress hormones: the costs of social status matter. *Anim. Behav.* 67, 591–602.
- Gruenewald, T.L., Kemeny, M.E., Aziz, N., 2006. Subjective social status moderates cortisol responses to social threat. *Brain Behav. Immun.* 20, 410–419.
- Hoek, H.N., Klein, H., Hoeck, P., 1982. Flexible social organization in hyrax. *J. Comp. Ethol.* 59, 265–298.
- Holekamp, K.E., Smale, L., 1998. Dispersal status influences hormones and behavior in the male spotted hyena. *Horm. Behav.* 33, 205–216.

- Holy, T.E., Guo, Z.S., 2005. Ultrasonic songs of male mice. *Plos Biol.* 3, 2177–2186.
- Hyman, J., 2003. Countersinging as a signal of aggression in a territorial songbird. *Anim. Behav.* 65, 1179–1185.
- Ketterson, E.D., Nolan, V., 1992. Hormones and life histories – an integrative approach. *Am. Nat.* 140, S33–S62.
- Koren, L., 2000. Hyrax socialization: first evidence for a matriarchal society. In Department of Zoology, Tel-Aviv University. MSc thesis.
- Koren, L., 2006. Vocalization as an indicator of individual quality in the rock hyrax. In Department of Zoology, Tel-Aviv University. PhD thesis.
- Koren, L., Mokady, O., Karaskov, T., Klein, J., Koren, G., Geffen, E., 2002. A novel method using hair for determining hormonal levels in wildlife. *Anim. Behav.* 63, 403–406.
- Koren, L., Mokady, O., Geffen, E., 2006. Elevated testosterone levels and social ranks in female rock hyrax. *Horm. Behav.* 49, 470–477.
- Kotiaho, J., Alatalo, R.V., Mappes, J., Parri, S., Rivero, A., 1998. Male mating success and risk of predation in a wolf spider: a balance between sexual and natural selection? *J. Anim. Ecol.* 67, 287–291.
- McComb, K., Reby, D., Baker, L., Moss, C., Sayialel, S., 2003. Long-distance communication of acoustic cues to social identity in African elephants. *Anim. Behav.* 65, 317–329.
- McElligott, A.G., Hayden, T.J., 1999. Context-related vocalization rates of fallow bucks, *Dama dama*. *Anim. Behav.* 58, 1095–1104.
- Mendelssohn, H., 1965. Breeding in the Syrian hyrax. *Int. Zoo Yearbook* 5, 116–125.
- Mooring, M.S., Patton, M.L., Lance, V.A., Hall, B.M., Schaad, E.W., Fetter, G.A., Fortin, S.S., McPeak, K.M., 2006. Glucocorticoids of bison bulls in relation to social status. *Horm. Behav.* 49, 369–375.
- Muller, M.N., Wrangham, R.W., 2004a. Dominance, aggression and testosterone in wild chimpanzees: a test of the 'challenge hypothesis'. *Anim. Behav.* 67, 113–123.
- Muller, M.N., Wrangham, R.W., 2004b. Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behav. Ecol. Sociobiol.* 55, 332–340.
- Ostner, J., Kappeler, P., Heistermann, M., 2008. Androgen and glucocorticoid levels reflect seasonally occurring social challenges in male redfronted lemurs (*Eulemur fulvus rufus*). *Behav. Ecol. Sociobiol.* 62, 627–638.
- Payne, R.S., McVay, S., 1971. Songs of humpback whales. *Science* 173, 585–597.
- Rasa, O.A.E., 1986. Coordinated vigilance in dwarf mongoose family groups: the 'watchman's song' hypothesis and the costs of guarding. *Ethology* 71, 340–344.
- Ryan, M.J., Tuttle, M.D., Rand, A.S., 1982. Bat predation and sexual advertisement in a neo-tropical anuran. *Am. Nat.* 119, 136–139.
- Sapolsky, R.M., 1982. The endocrine stress-response and social-status in the wild baboon. *Horm. Behav.* 16, 279–292.
- Sapolsky, R.M., 1993. Endocrinology alfresco – psychoendocrine studies of wild baboons. *Recent Progress in Hormone Research*, 48, pp. 437–468.
- Spector, D.A., 1994. Definition in biology – the case of bird song. *J. Theor. Biol.* 168, 373–381.
- Sapolsky, R.M., 2005. The influence of social hierarchy on primate health. *Science*. 308, 648–652.
- Tenaza, R.R., 1976. Songs, choruses and countersinging of Kloss gibbons (*Hylobates klossii*) in Siberut-Island, Indonesia. *J. Comp. Ethol.* 40, 37–52.
- Titze, I.R., 2000. Principles of Vocal Production. Nationally Center for Voice and Speech, Iowa City.
- Tuttle, M.D., Ryan, M.J., 1982. The role of synchronized calling, ambient light, and ambient noise, in anti-bat-predator behavior of a treefrog. *Behav. Ecol. Sociobiol.* 11, 125–131.
- Vleugels, M.P., Eling, W.M., Rolland, R., Degraaf, R., 1986. Cortisol-levels in human-pregnancy in relation to parity and age. *Am. J. Obstet. Gynecol.* 155, 118–121.
- Wagner, W.E., 2005. Male field crickets that provide reproductive benefits to females incur higher costs. *Ecol. Entomol.* 30, 350–357.
- Walcott, C., Mager, J.N., Piper, W., 2006. Changing territories, changing tunes: male loons, *Gavia immer*, change their vocalizations when they change territories. *Anim. Behav.* 71, 673–683.
- Yang, H.Z., Lan, J., Meng, Y.J., Wan, X.J., Han, D.W., 1998. A preliminary study of steroid reproductive hormones in human hair. *J. Steroid Biochem. Mol. Biol.* 67, 447–450.
- Zahavi, A., 1977. Cost of honesty (further remarks on handicap principle). *J. Theor. Biol.* 67, 603–605.